

THE EGGS OF *Aedes funereus*, *Aedes notoscriptus* AND
Aedes alternans (DIPTERA: CULICIDAE)

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Abstract.—Scanning electron micrographs are used to provide descriptions of the eggs of *Aedes (Verrallina) funereus*, *Ae. (Finlaya) notoscriptus* and *Ae. (Mucidus) alternans*. In the egg of *Ae. funereus* the outer chorionic cells of the ventral (upper) and dorsal (lower) surfaces differ markedly in structure, but the egg's most distinct features are its pronounced narrowness relative to length, and the unusually large micropylar disk. Ventral and dorsal surfaces also differ very substantially in *Ae. notoscriptus*, the dorsal surface being particularly interesting as its structure probably represents an early stage in the development of long, dorsal surface filaments as seen in other species of the subgenus *Finlaya*. The *Ae. alternans* egg is wide in relation to length and its entire surface is much more uniform. Some data are presented on the variation found between 5 individual eggs from each species.

Key Words: Insecta, eggs, mosquito, fine structure

The three *Aedes* species whose eggs are described in this paper are all from the Australasian Region. As such, their taxonomy, distribution, biology and importance as pests and/or disease vectors have all been comprehensively treated elsewhere (*Ae. (Verrallina) funereus* (Theobald), Lee et al. 1987, p. 276; *Ae. (Finlaya) notoscriptus* (Skuse), Lee et al. 1982, p. 196; *Ae. (Mucidus) alternans* (Westwood), Lee et al. 1984, p. 73).

No previous description of the egg of *Ae. funereus* has been given. Graham (1929) provided the first observations on the egg of *Ae. notoscriptus* at the stereomicroscopic level, and Pillai (1962) investigated the structure of the egg shell and the egg's ability to resist desiccation. The egg of this important species has never been completely described, however, and not at all at the electron microscopic level. A very early account of the egg of *Ae. alternans*, but with illus-

trations limited to outline drawings, was given by Colledge (1904) and was used by Mattingly (1970) in his comparison of eggs of several species of the subgenus *Mucidus*. The egg shell and its resistance to drying were studied by Pillai (1962), but details of the fine structure have never been presented.

In this paper we describe the eggs of these three species with the aid of scanning electron micrographs. Since numerous eggs were available, opportunity also was taken to look at intraspecific structural variation in the outer chorionic cells by examining 5 individual eggs of each species and recording selected measurements. The 5 eggs in each case were not certainly from different females, but to optimize the probability that they were, eggs were taken from different egg papers where possible, or from widely separated positions on the same paper.

MATERIALS AND METHODS

Eggs were obtained from females collected in the field and induced to oviposit on wet filter paper in the laboratory. Each paper bearing eggs was folded to line the inside (eggs on inner surface) of a small plastic petri dish and the paper moistened before mailing to Vero Beach. On arrival, eggs were mounted for microscopy either by cutting out small pieces of paper with attached eggs and sticking these to double-sided sticky tape already attached to stubs, or by lifting individual eggs on a very fine artist's brush and laying them on sticky tape in the required position. Eggs were dried completely over calcium chloride for 0.5 h, then sputter coated with gold. Microscopy was done in a Hitachi S-510 scanning electron microscope.

In the study of intraspecific structural variation, the area selected for examination was the chorion on the ventral surface, in the middle of the egg. Particular care was taken to obtain micrographs of an exactly equivalent area in each of the 5 eggs selected for each species. Micrographs at 1000 \times and 1500 \times were taken, the one at lower magnification to include more chorionic cells for counting numbers of tubercles and measuring cell dimensions, the other at higher magnification for measuring tubercles. Of the two cell dimensions, length was the distance between the two most widely separated cell corners aligned approximately longitudinally (anterior/posterior) with respect to the egg (see Fig. 15). Width was taken at the widest point circumferentially with respect to the egg (whether or not exactly coincident with two cell corners). Tubercle diameters were measured at the base at the widest point, except for the large tubercles in *Ae. notoscriptus*, where the upper portion of each tubercle was measured as it was often distinctly narrower than the base (see Fig. 9c, e, 15) and easily distinguishable. Tests for differences between eggs with respect to means of all measurements were done by

the GT2 method (Sokal and Rohlf 1981), in some cases after transformation to normalize the distributions (see later). The distributions of large tubercle numbers in *Ae. funereus* and *Ae. alternans* (Fig. 3) were not assumed to be normal and the Kruskal-Wallis method was used to test for differences between eggs. Means given in the text are with attached standard errors and were calculated from an equal number of measurements from each of the 5 eggs of each species.

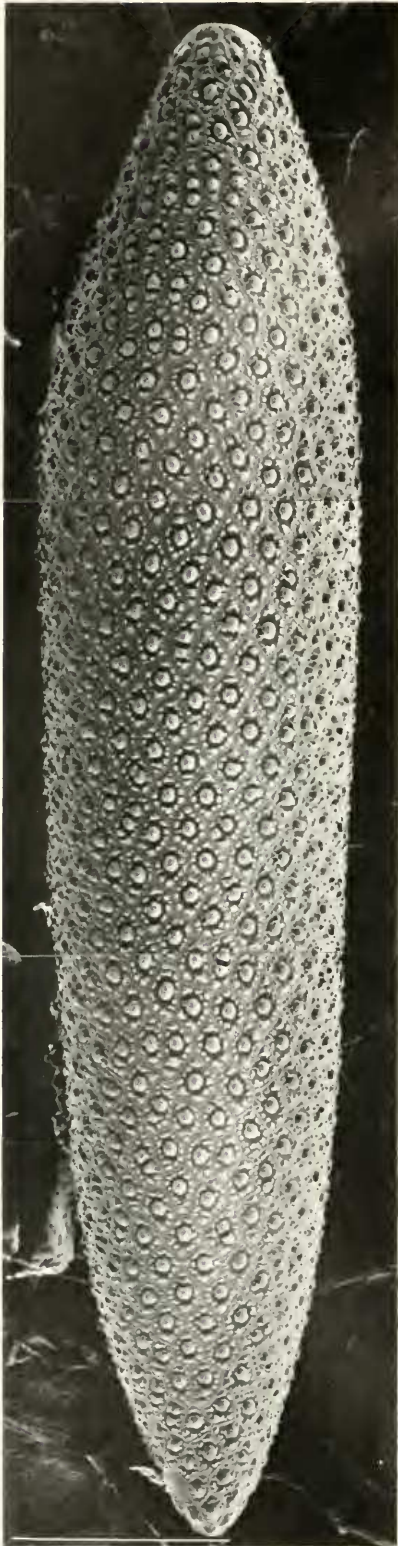
In the terminology we have followed Harbach and Knight (1980), except for "outer chorionic cell field" (Linley 1989), and "micropylar dome," defined as a dome-shaped area with distinct margin surrounding the micropyle and within the micropylar disk.

RESULTS

Aedes (Verrallina) funereus (Figs. 1, 2, 6, 7, 15)

Size: dimensions as in Table 1. Color: dull black. Overall appearance: cigar-shaped and long in relation to width (Fig. 1, Table 1). Dorsal (lower) side flatter, ventral (upper) side more curved (Fig. 2a). Tapered anterior end somewhat conical, widest at about anterior 0.25, then slightly tapered posteriorly until posterior 0.25, then markedly so (Fig. 1). Posterior end rather sharply pointed in some eggs, less so in others. Micropylar collar indistinct. Outer chorionic cells regular in appearance, most with single, large central tubercle and several small peripheral ones (Fig. 1)

Chorion, ventral (upper) surface: outer chorionic cells mostly hexagonal, occasionally pentagonal, rarely quadrilateral, outlines variable (Figs. 2d, 15). Cell length (mean $25.3 \pm 0.4 \mu\text{m}$, $n = 50$) greater than width (mean $15.0 \pm 0.3 \mu\text{m}$, $n = 50$), cell fields about $2.7 \mu\text{m}$ less in each dimension. Most cells with single large tubercle, some with 2 or rarely 3 (Figs. 3, 15), mean tubercle diameter $5.97 \pm 0.14 \mu\text{m}$ ($n = 50$), range 2.9–7.6 μm . Structurally, each tubercle made



up of a base with shallow peripheral excavations, walls smooth and vertical or nearly so (Fig. 2d, e, f), capped by dome-shaped upper portion covered with close-packed more or less round nodules (Fig. 2e, f). Surrounding cells field smooth, with slight striations appearing only at high magnification (Fig. 2e, f). Small tubercles confined to periphery of cell field, adjacent to outer chorionic reticulum (Figs. 2d, 15), mean number per cell 18.1 ± 0.4 ($n = 50$), range 10–24, diameter $0.6\text{--}3.3 \mu\text{m}$, size distribution skewed (Fig. 4). Regression of small tubercle diameter on number highly significant ($P < 0.005$), diameter smaller as number increases (Fig. 5). Small tubercle shape highly irregular, each tapering upward from smooth base to a narrower top; tops tending to be smooth, but progressively larger ones with increasingly numerous small nodules (Fig. 2d, e, f). Groups of small tubercles often joined by bridges and some similarly joined to large tubercles (Fig. 2d, e). Outer chorionic reticulum low, width $2.5\text{--}3.6 \mu\text{m}$, consisting of a fine reticulated mesh (Fig. 2e, f), with central line of bead-like prominences, diameter $0.3 \mu\text{m}$, $0.7\text{--}2.6 \mu\text{m}$ apart. Reticulum mesh often partially covering lower sides of closely adjacent small tubercles (Fig. 2e, f).

Chorion, lateral surface (ventral-dorsal transition): down lateral surfaces of egg chorionic cells become more irregular in form and, unlike ventral surface, progressively longer circumferentially than longitudinally (Fig. 6a, b). Large tubercles progressively become more numerous with nodular surfaces less distinct. Tubercles at first remain more centrally positioned in cell, then displace small tubercles around edges of cell field (Fig. 6a, c, d). In lower (more dorsal) portion of transition (Fig. 6b), small tubercles almost disappear, large tubercles be-

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Fig. 1. *Ac. funereus*. Entire egg, ventral (upper) view, anterior end at top. Scale = $100 \mu\text{m}$.

Table 1. Dimensions of eggs of three species of *Aedes* (n = 10).

Species	Length (μm)		Width (μm)		L/W ratio	
	$\bar{x} \pm \text{SE}$	Range	$\bar{x} \pm \text{SE}$	Range	$\bar{x} \pm \text{SE}$	Range
<i>Ae. funereus</i>	770.3 \pm 14.6	707.1–848.5	171.9 \pm 3.1	151.5–186.9	4.50 \pm 0.13	3.88–5.21
<i>Ae. notoscriptus</i>	629.0 \pm 19.5	517.7–722.2	179.1 \pm 4.2	154.0–199.5	3.52 \pm 0.09	2.93–3.86
<i>Ae. alternans</i>	773.5 \pm 7.4	732.3–808.1	379.8 \pm 8.1	351.0–421.7	2.04 \pm 0.03	1.92–2.20

come smaller, smooth-topped and more numerous, usually contiguously aligned in the longitudinally narrow cells (Fig. 6b, e). Outer chorionic reticulum changes in this region from fine mesh form of ventral surface (Fig. 6c, d) to narrower form with only faint surface striations and more distinct edges (Fig. 6e).

Chorion, dorsal (lower) surface: chorionic cells much narrower longitudinally than circumferentially. Tubercles small, low and clustered mostly away from cell edges (Fig. 6b, f), rounded surfaces smooth. Reticulum narrow width 0.8–1.7 μm , surface slightly rough or with very indistinct striations (Fig. 6f).

Anterior end, micropyle: chorionic cells become smaller towards anterior end, small tubercles fewer and, just posterior to collar, often joined to large tubercle by sheet-like strips, partly occluding cell field (Fig. 7a, b). On dorsal (lower) surface, cells close to micropyle contain fairly large peripheral tubercles (Fig. 7c), these rapidly undergoing transition to typical dorsal type a short distance posteriorly (Fig. 7c). Micropylar collar conforming to overall taper of egg and therefore inconspicuous, continuous (Fig. 2b, c), height variable, 3–22 μm , surface with chorionic cell outlines visible (Fig. 7b). Collar diameter 30–37 μm , wall width 2–3.5 μm , almost always narrower on dorsal side (Fig. 2b), surface somewhat rough and pitted (Fig. 2c), internal diameter 24–28 μm , inner wall with very shallow indentions (Fig. 2b, c). Micropylar disk very large (Fig. 2b, c), diameter 20–23 μm , edge very distinct and raised, surrounded by narrow furrow (Fig. 2c), micropylar dome present but in-

conspicuous (Fig. 2c), diameter about 14 μm , micropylar orifice trilobed (Fig. 2c), diameter 2.3 μm , surrounded by evenly spaced, low, radial walls, about 2.3 μm long (Fig. 2c).

Posterior end: chorionic cells smaller towards posterior end, small tubercles fewer (Fig. 7d), nodular surface of large tubercles becoming smoother, completely so at very end of egg (Fig. 7d, e). Central prominences of reticulum becoming joined by progressively raised, conspicuous ridge (Fig. 7d). Tubercles in cells at posterior end on dorsal (lower) surface fused, smooth-surfaced (Fig. 7f), rapidly becoming more conspicuous and separate anteriorly (Fig. 7f) to conform with typical dorsal structure.

Aedes (Finlaya) notoscriptus
(Figs. 8–11, 15)

Size: dimensions as in Table 1. Color: dull black. Overall appearance: very broadly cigar-shaped, widest at about anterior 0.25, from this point roundly tapered anteriorly, posteriorly tapered slightly to posterior 0.25, then taper increases rapidly to end of egg (Fig. 8). Micropylar collar fairly distinct. Outer chorionic cells regular, appearing small relative to size of egg. Each cell with one large, more or less round and protruding tubercle, giving stereomicroscopically viewed eggs a bumpy appearance.

Chorion, ventral (upper) surface: outer chorionic cells usually hexagonal, but often pentagonal (Figs. 9c, 15). Cell length (mean 18.2 \pm 0.4 μm , n = 50) usually slightly less than width (mean 19.4 \pm 0.3 μm , n = 50), cell fields about 3.0 μm less in each dimension. All cells with only one large tubercle,

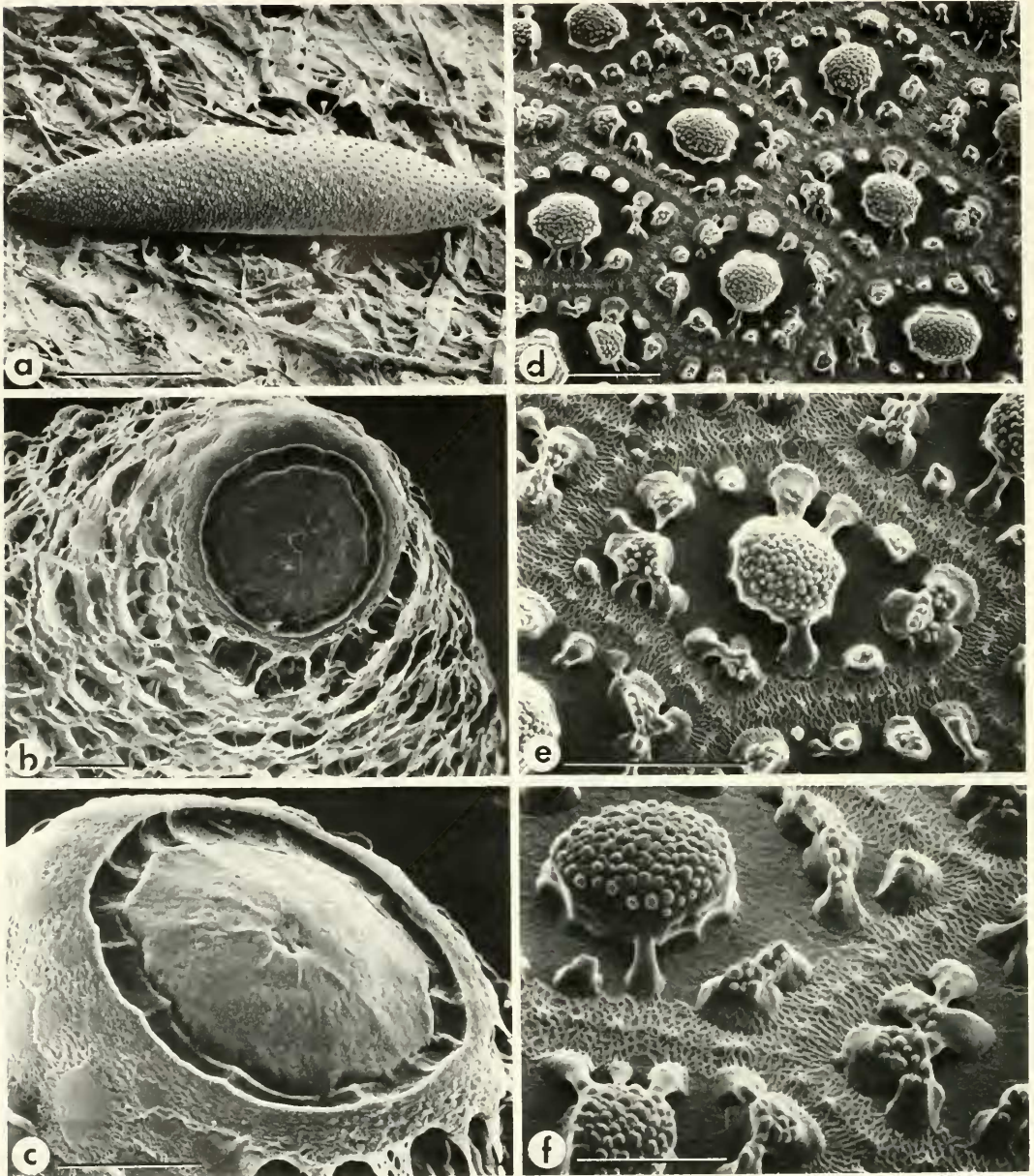
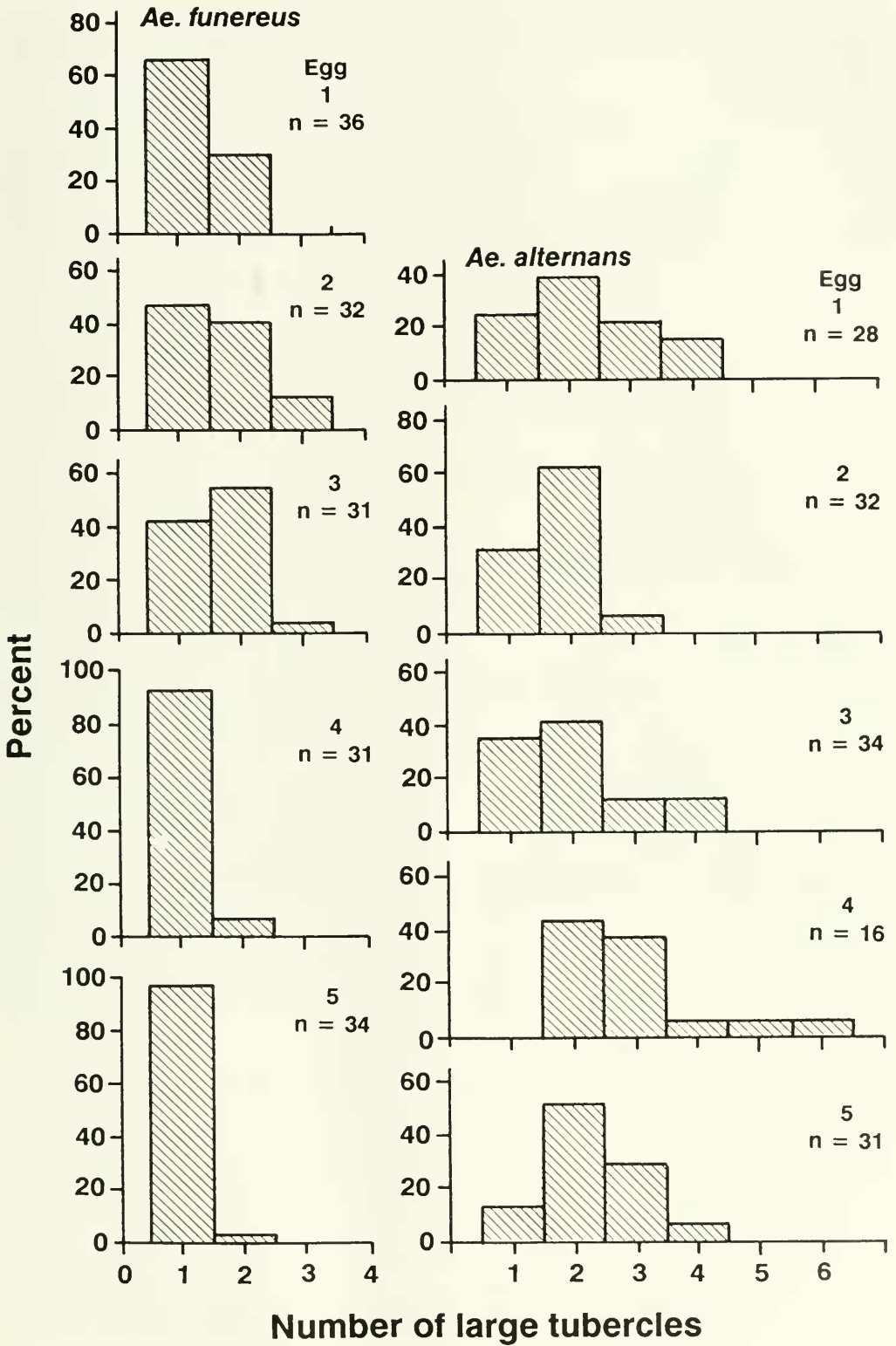


Fig. 2. *Ae. funereus*. (a) Whole egg, lateral view, anterior end at right; (b) anterior end and micropylar apparatus; (c) detail, micropylar apparatus; (d) typical outer chorionic cells, ventral surface, middle of egg; (e) detail, single chorionic cell; (f) detail, large and small tubercles and outer chorionic reticulum. Scale = 200 μm (a), = 10 μm (b, c, d, e), = 5 μm (f).

Fig. 3. *Ae. funereus*, *Ae. alternans*. Distributions of numbers of large tubercles.



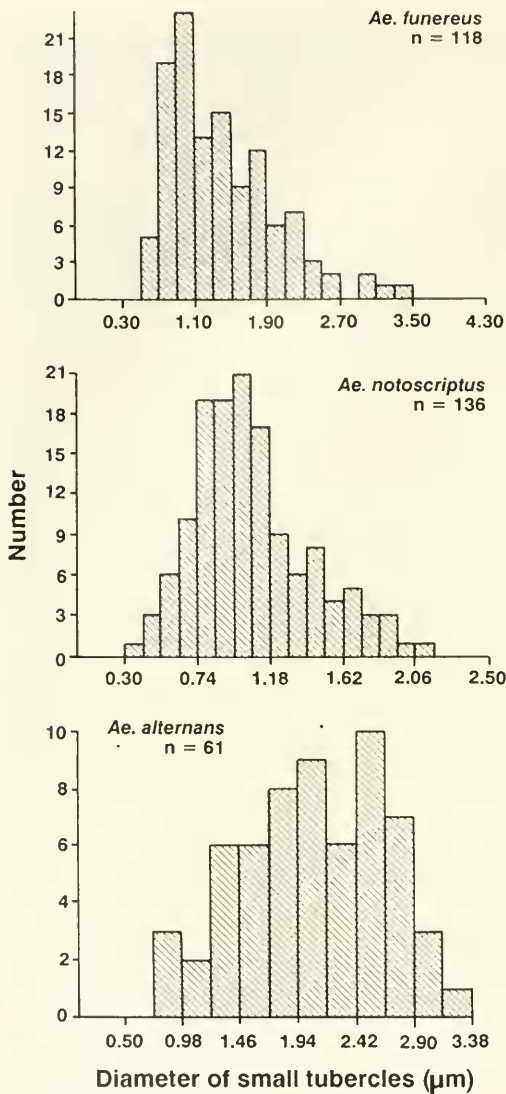


Fig. 4. *Ae. funereus*, *Ae. notoscriptus*, *Ae. alternans*. Distributions of small tubercle diameter.

mean diameter $5.65 \pm 0.18 \mu\text{m}$ ($n = 50$), range $3.52\text{--}8.23 \mu\text{m}$. Each tubercle consisting of a base, with round or irregular periphery (Figs. 9c, 15) and smooth, rounded walls, supporting a smaller, usually more circular cap ornamented with round or irregular nodules (Fig. 9c, d, e). Cap often of considerably smaller diameter than base, especially in mid-ventral line (Fig. 9c, 15).

Cell fields smooth except for scattered minute tubercles (Fig. 9d). Many small tubercles present, those away from edges of reticulum tending to be smaller and loosely organized in rings around large tubercle (Fig. 9d, e), those adjacent to reticulum larger, especially in cell corners (Figs. 9d, e, 15). Mean number of small tubercles 18.8 ± 1.2 ($n = 50$), range 9–55, diameter $0.32\text{--}2.71 \mu\text{m}$, size distribution skewed (Fig. 4), shape usually round, domed or peaked (Fig. 9d, e), larger ones more irregular. Outer chorionic reticulum $2.5\text{--}4.5 \mu\text{m}$ wide, low and complex, consisting of an intricate basal meshwork (Fig. 9d) in some sections overlain by a second mesh perforated by pores (Fig. 9d, e).

Chorion, lateral surface (ventral-dorsal transition): ventral-type cells as described above found only in a strip 4–5 cells wide in mid-ventral line (Figs. 8, 9c). Cells to either side in upper lateral regions become distinctly wider circumferentially than longitudinally (Fig. 9a), small tubercles close to large central tubercle joined to it by narrow, spoke-like bridges, peripheral small tubercles often similarly joined to reticulum (Fig. 9a, f). About half way down sides of egg, cells undergo abrupt transition to dorsal type; transitional cells either with single large tubercle having thickened spokes (Fig. 9b), with thin spokes ventrally but dorsal cell field occluded by smooth continuous sheet (Fig. 9a, b), or cells with several moderately large tubercles and a few smaller ones (Fig. 9a, b). Tiny tubercles in cell fields larger, and present also in reticulum, which has pronounced central ridge (Fig. 9b).

Chorion, dorsal (lower) surface: chorionic cells distinctly wider circumferentially than longitudinally, often pentagonal (Fig. 10a). Each cell peripherally composed of $18\text{--}26$ (mean 20.7 ± 0.7 , $n = 10$) contiguous, medium-sized tubercles topped by a continuous ridge. Enclosed cell fields with $18\text{--}31$ (mean 24.7 ± 1.0 , $n = 10$) more or less round, or occasionally irregular tubercles (Fig. 10a, b), diameter $0.7\text{--}2.4 \mu\text{m}$ (mean

$1.7 \pm 0.1 \mu\text{m}$, $n = 20$), surfaces smooth or slightly uneven (Fig. 10b). Spaces between tubercles occupied by small, button-like tubercles, and these also covering reticulum (width $1.6\text{--}3.3 \mu\text{m}$), but less prominent on low central ridge (Fig. 10b). Dorsal type cells typically as just described, but occasionally with fewer, scattered tubercles, vacant spaces filled by very small tubercles (Fig. 10c).

Anterior end, micropyle: chorionic cells smaller approaching anterior end, cell fields become occluded, large tubercles less conspicuous, surfaces smoother, spokes in more lateral cells fewer (Fig. 11a, b). Dorsal (lower) surface transition from micropylar collar to typical dorsal cell structure rapid, and as illustrated (Fig. 11c). Micropylar collar fairly prominent, almost always continuous, outer walls often rounded (Fig. 11a, c), height $7\text{--}11 \mu\text{m}$, diameter $36\text{--}41 \mu\text{m}$, wall width $5\text{--}11 \mu\text{m}$, surface rough and pitted (Fig. 11d, e), internal diameter $21\text{--}24 \mu\text{m}$, internal wall with shallow excavations (Fig. 11e). Micropylar disk small, boundary very clearly demarcated (Fig. 11e), surface rough, diameter $7\text{--}9 \mu\text{m}$, micropylar orifice trilobed, diameter $2.7 \mu\text{m}$.

Posterior end: chorionic cells become smaller approaching posterior end, small tubercles and spokes connected to large tubercles fewer, cell fields increasingly occluded, totally so at extreme end (Fig. 10d, e), large tubercles at end smooth surfaced, irregularly shaped (Fig. 10d, e). On dorsal (lower) surface, typical dorsal type cells present almost to extreme end of egg (Fig. 10f).

Aedes (Mucidus) alternans
(Figs. 12–14, 15)

Size: dimensions as in Table 1. Color: dull black. Overall appearance: rhomboidal in ventral (Fig. 12) or dorsal view, widest just anterior to 0.5 of length, width, relatively great with respect to length. Shape in lateral view similar, but curvature of ventral surface greater than dorsal (Fig. 13a). Micropylar collar distinct (Fig. 12), outer chori-

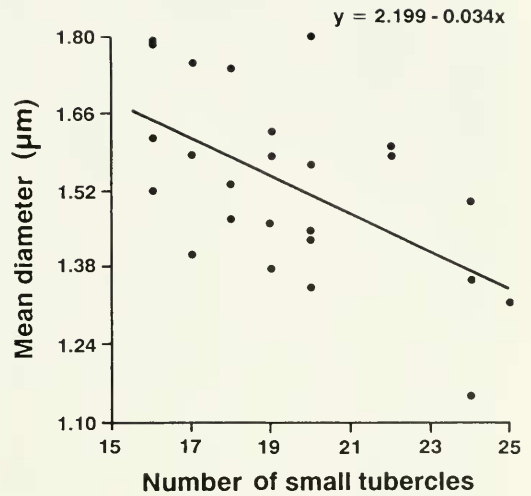


Fig. 5. *Ae. funereus*. Regression of mean diameter of small tubercles on number of small tubercles in cell.

onic cells appearing uniform over whole egg surface.

Chorion, ventral, lateral and dorsal surfaces: all surfaces very similar. Structure typified by and described for cells on ventral (more curved) surface, with comments on lateral and dorsal surface differences, as follows. Shape of cells quite irregular, mostly pentagonal, occasionally hexagonal or quadrilateral (Fig. 13b), length (mean $22.2 \pm 0.5 \mu\text{m}$, $n = 50$) greater than width (mean $16.3 \pm 0.4 \mu\text{m}$, $n = 50$). Shape of lateral (Fig. 13c) and dorsal (Fig. 13d) surface cells similar, but dimensions somewhat smaller, especially on dorsal surface. Cell fields about $2.0 \mu\text{m}$ smaller in each dimension. Two large tubercles most frequently present, but numbers variable between eggs (Fig. 3). Tubercles in larger ventral cells in some instances more centrally placed, but in others more towards edges of cell field (Fig. 13b, f); tubercles always tending to be centrally placed in smaller lateral (Fig. 13c, g) and especially dorsal (Fig. 13d, h) cells. Mean diameter of large tubercles $5.64 \pm 0.12 \mu\text{m}$ ($n = 50$), range $3.2\text{--}7.6 \mu\text{m}$. Each tubercle constructed of an irregularly polygonal base, each side shallowly indented (Fig. 13g, i), with smooth

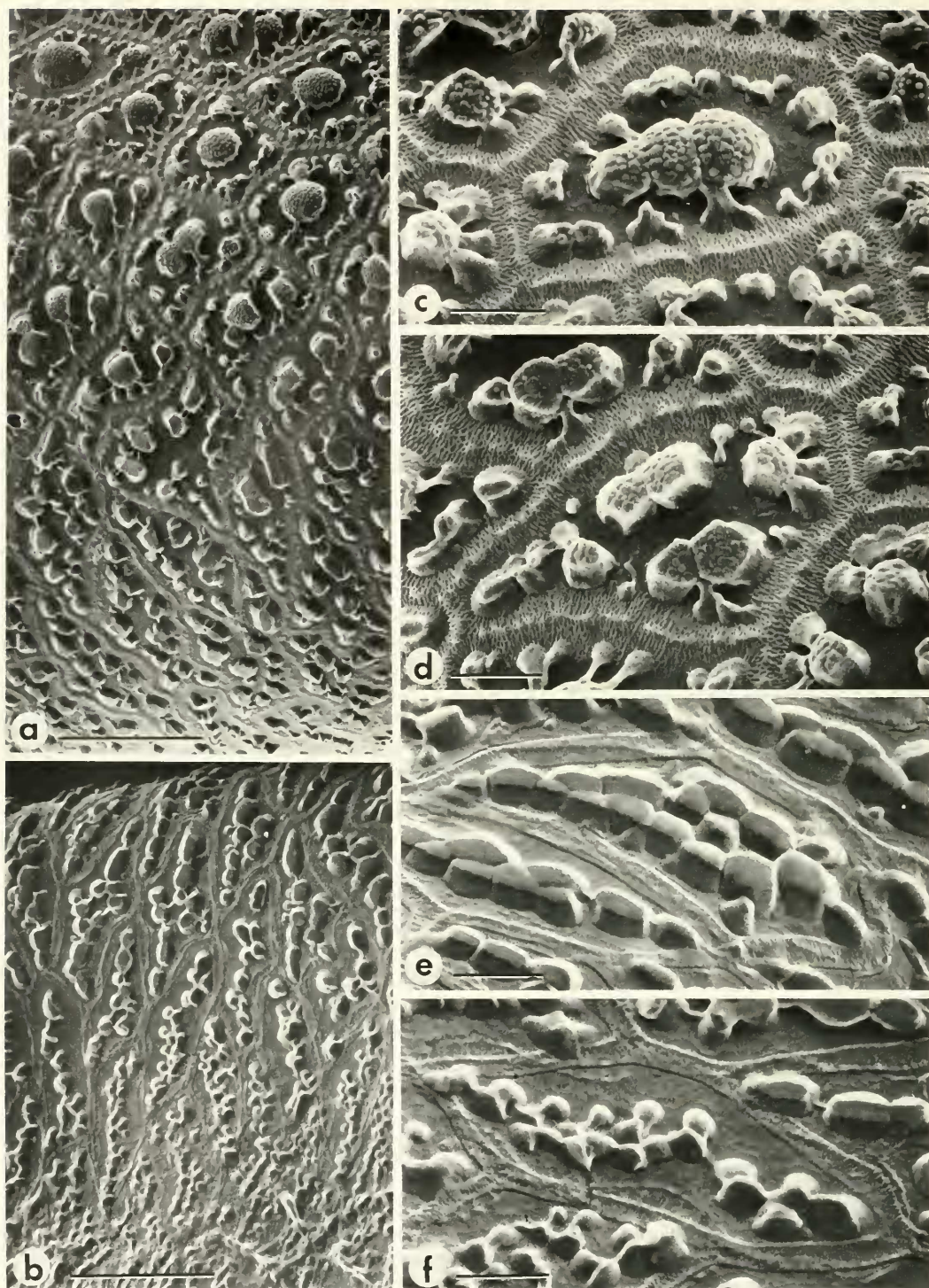


Fig. 6. *Ae. funereus*. (a) Upper (more ventral) portion of ventral-dorsal transition, middle of egg; (b) lower (dorsal) portion of ventral-dorsal transition; (c) outer chorionic cell detail, ventral-lateral portion of transition; (d) cell detail, lateral portion of transition; (e) cell detail, lateral-dorsal portion of transition; (f) cell detail, dorsal (lower) surface. Scale = 20 μm (a, b), = 5 μm (c, d, e, f).

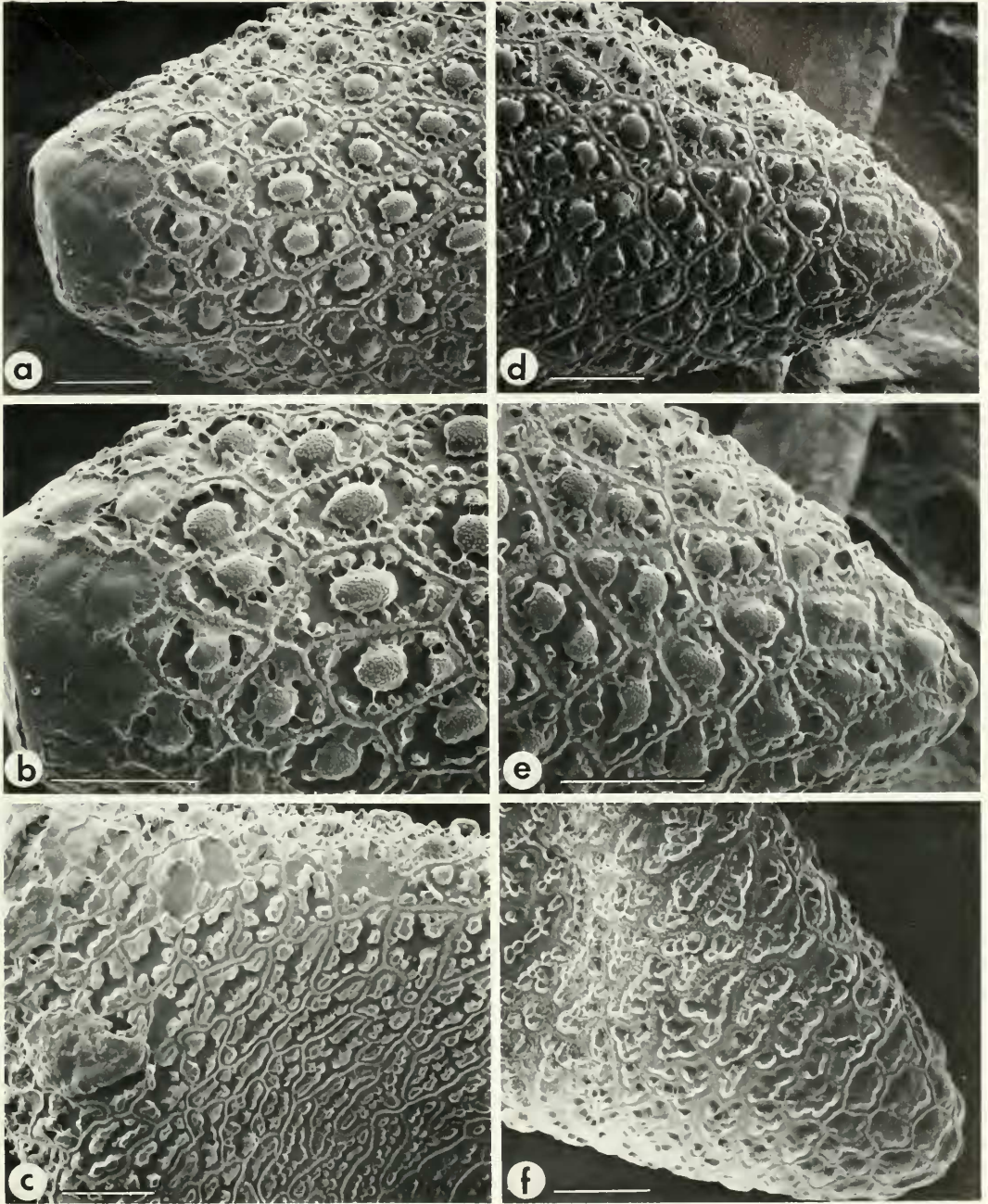
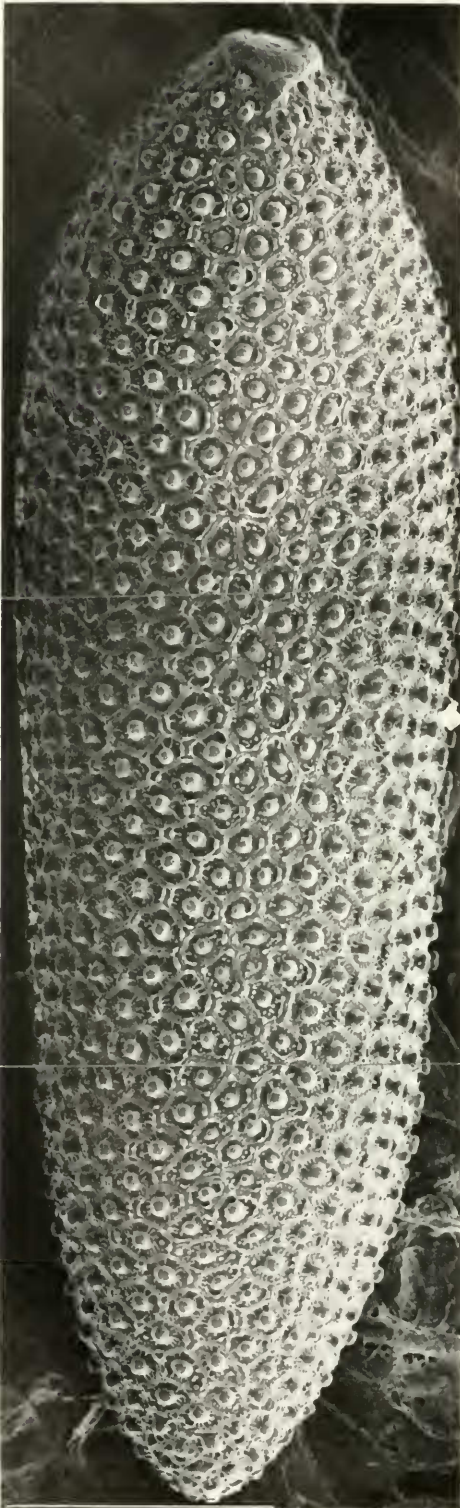


Fig. 7. *Ae. funereus*. (a) Anterior end, ventral surface; (b) anterior end, outer chorionic cell detail; (c) anterior end, dorsal surface; (d) posterior end, ventral view; (e) posterior end, outer chorionic cell detail; (f) posterior end, dorsal surface. Scale = 20 μ m.



and vertical walls, supporting a usually more rounded but occasionally polygonal cap. Cap surface with flat nodules separated by fissures or pits (Fig. 13f, i). Cell fields appearing smooth at low magnification (Fig. 13f, g, h), but densely packed tiny tubercles visible at greater enlargement (Fig. 13e). Small tubercles restricted to cell periphery (Fig. 13b, f, g), mean number per cell 9.8 ± 0.3 ($n = 50$), range 5–17, more numerous in ventral surface cells, less so in lateral and particularly dorsal cells (Fig. 13b, c, d). Size distribution normal (Fig. 4), mean diameter $2.18 \pm 0.09 \mu\text{m}$ ($n = 50$), range 0.7–4.3 μm . Bases of small tubercles usually much wider than tops (Fig. 13f, g, h), walls smooth, top surfaces very irregularly shaped, slightly rough, similar to surfaces of large tubercles. Small tubercles frequently joined to large ones by narrow bridges (Fig. 13f, g). Outer chorionic reticulum low, width 1.7–4.5 μm , very variable. Structure also variable and complex, consisting of an intricate basal meshwork with central row of beadlike projections (Fig. 13g, h, i), 0.5–0.8 μm in diameter 0.9–3.0 μm apart, which may or may not be overlain by a second, raised and perforated meshwork (Fig. 13e, f). Reticulum usually overlying outsides of small tubercle bases (Fig. 13g, h, i).

Anterior end, micropyle: chorionic cells become progressively smaller towards anterior end. Often only a single large tubercle present, or, if tubercles multiple, closely spaced or contiguous (Fig. 14a, b). Tops of large tubercles rounder, number of small tubercles fewer, almost all having bridges to large tubercle(s) (Fig. 14a, b). Micropylar collar conspicuous, rarely continuous, one or two deeply notched gaps usually present (Fig. 14c, d), outer wall rounded (Fig. 14a, b). Collar height 11–14 μm , diameter 46–54 μm , wall width 8–12 μm , anterior surface

Fig. 8. *Ae. notoscriptus*. Entire egg, ventral (upper) view, anterior end at top. Scale = 100 μm .

Table 2. Attributes of five individual eggs from three species of *Aedes*. Means arranged in ascending order of magnitude, egg numbers shown at left in each column. Means followed by the same letter do not differ significantly.

Species	Diameter of Large Tubercles (μm)			No. of Small Tubercles			Diameter of Small Tubercles (μm)			Ratio Cell Length/Cell Width		
	Egg	n	\bar{x}	Egg	n	\bar{x}	Egg	n	\bar{x}	Egg	n	\bar{x}
<i>Ae. funereus</i>	2	27	5.46a	2	29	17.2a	1	118	1.40a	4	15	1.45a
	1	22	5.78a	4	28	17.3a	3	103	1.51a	5	15	1.53a
	3	21	5.90a	1	27	17.4a	5	102	1.52a	1	15	1.71a
	5	19	6.19a	5	29	18.6a	2	92	1.56a	3	15	1.75a
	4	14	6.50b	3	26	18.8a	4	90	1.65b	2	15	2.20b
<i>Ae. notoscriptus</i>	4	11	4.42a	1	14	14.3a	4	123	0.96a	1	15	0.88a
	1	16	5.23ab	3	15	16.3a	3	129	0.99a	4	15	0.88a
	3	14	5.79bc	2	12	17.3a	1	92	1.00a	3	15	0.97a
	2	12	5.95bc	4	15	17.4a	5	290	1.01a	2	13	0.99a
	5	13	6.85c	5	19	30.3b	2	136	1.07b	5	15	1.05b
<i>Ae. alternans</i>	3	29	5.08a	3	34	8.7a	1	62	2.04a	3	15	1.24a
	1	34	5.31ab	5	31	8.9a	2	61	2.06a	2	15	1.38a
	5	37	5.36ab	2	32	10.5b	3	51	2.16a	1	15	1.44a
	2	39	5.77bc	1	28	11.1bc	4	68	2.23a	4	15	1.46a
	4	30	6.13c	4	16	12.6c	5	50	2.33a	5	15	1.46a

slightly rough (Fig. 14d), internal diameter 31–36 μm , inner wall quite shallow, perimeter slightly indented (Fig. 14c, d). Micropylar disk clearly defined, edge raised, step-like (Fig. 14c, d), diameter 23–26 μm . Micropylar dome distinct (Fig. 14c, d), diameter about 15 μm , orifice slightly trilobed, diameter about 2.9 μm .

Posterior end: Chorionic cells smaller approaching posterior end, number of small tubercles fewer (Fig. 14e), large tubercles become progressively fused, becoming single, complex, smooth-surfaced tubercle at extreme end (Fig. 14f).

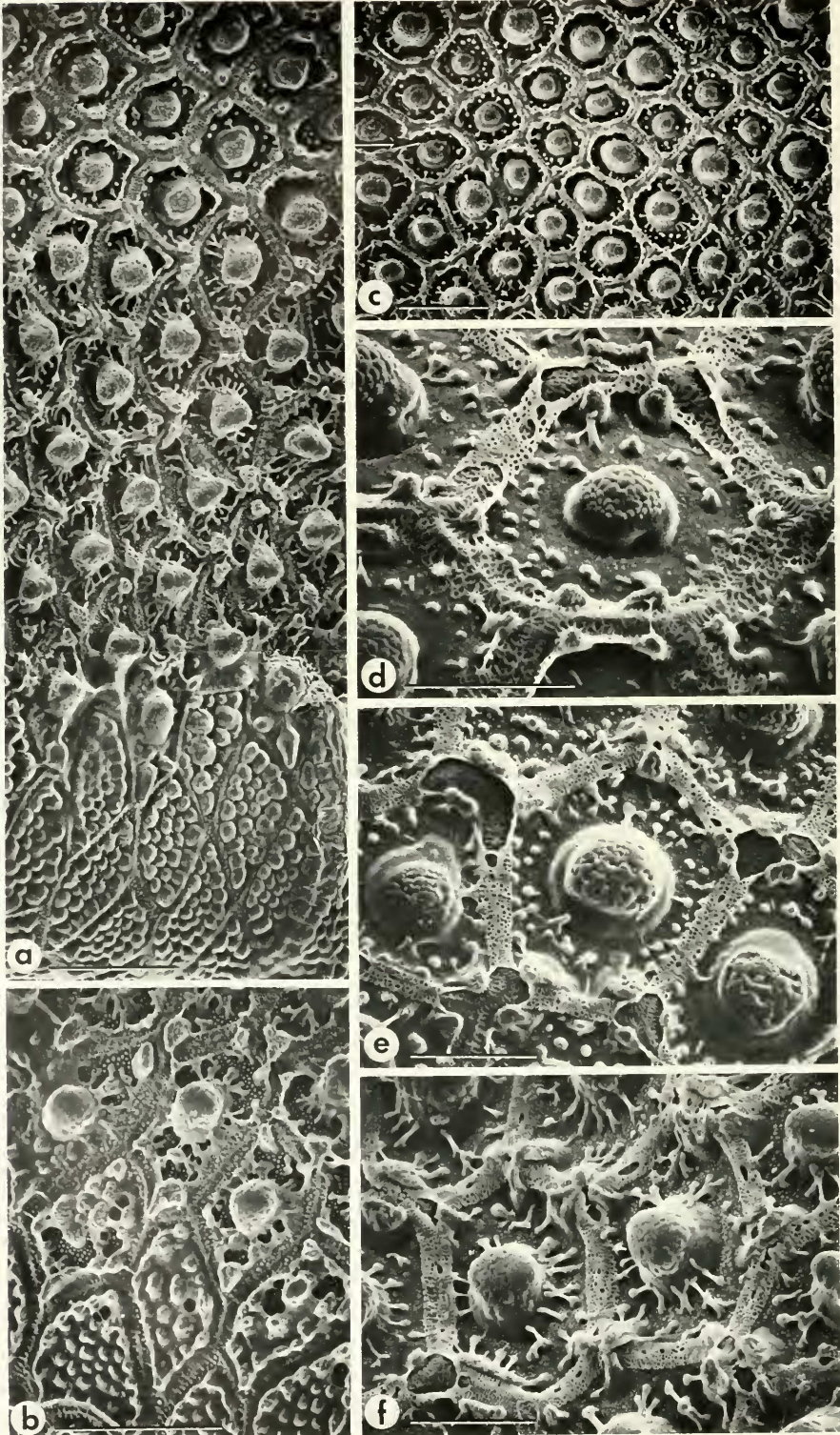
INTRASPECIFIC VARIATION

Representative areas of the outer chorion in the mid-ventral region from each of the 5 individual eggs from each species are shown in Fig. 15. All measurements of cell size and numbers and diameters of large and small tubercles were made from larger areas of chorion in this region. Data for 5 characteristics were collected; number of large tubercles (*Ae. funereus* and *Ae. alternans* only, shown in Fig. 3), and number of small

tubercles, diameter of small and large tubercles, and cell length/width ratio (Table 2). Statistical comparisons of small tubercle diameter for *Ae. funereus* and *Ae. notoscriptus* were done after normalizing the skewed distributions (Fig. 4) by \log_{10} transformation, but means are expressed in μm in Table 2.

There were significant differences between eggs with respect to large tubercle numbers (Fig. 3) in both *Ae. funereus* ($P < 0.001$) and *Ae. alternans* ($P < 0.005$). These differences are visible to some extent in Fig. 15 (cf. Fig. 3) despite the relatively small area of chorion shown. In *Ae. funereus*, large tubercles were more numerous in those eggs (2, 3, Fig. 3) in which the chorionic cells were longer relative to width (Fig. 15, and see length/width ratios in Table 2). The same was generally true of *Ae. alternans*, where eggs 1, 4 and 5 had more large tubercles (Fig. 3) and the greatest ratios (Table 2). *Aedes notoscriptus* cells invariably had a single large tubercle (Fig. 15).

In all three species, eggs differed significantly in terms of large tubercle diameter



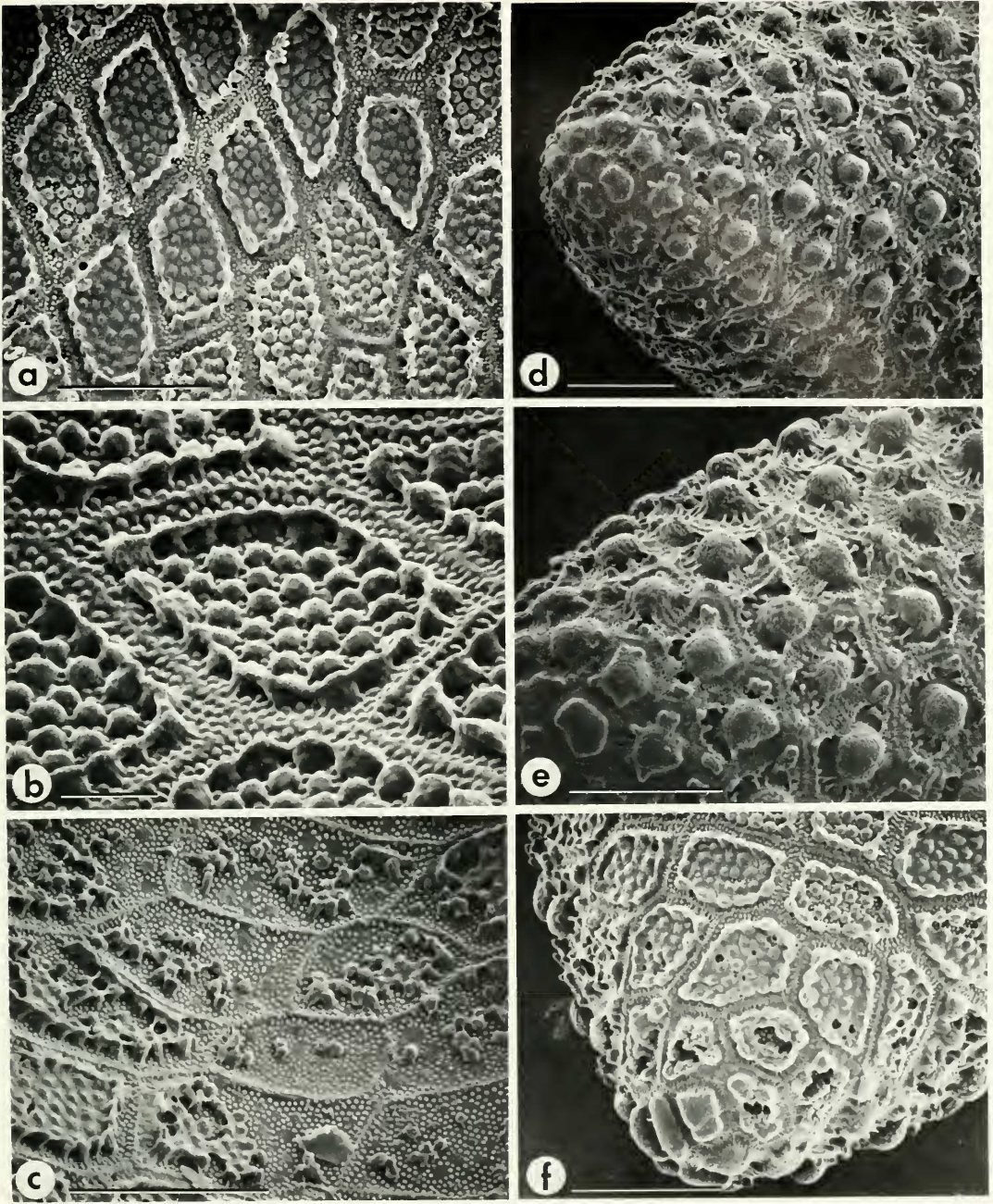


Fig. 10. *Ae. notoscriptus*. (a) Outer chorionic cells, dorsal surface; (b) detail, chorionic cell, dorsal surface; (c) variant cells, dorsal surface; (d) posterior end, ventral surface; (e) posterior end, outer chorionic cell detail; (f) posterior end, dorsal surface. Scale = 20 μm (a, c, d, e, f), = 5 μm (b).

Fig. 9. *Ae. notoscriptus*. (a) Entire ventral-dorsal transition, middle of egg; (b) detail, lateral-dorsal portion of transition; (c) outer chorionic cells, ventral surface, middle of egg; (d) detail, chorionic cell and reticulum, mid-ventral surface; (e) detail, chorionic cell and reticulum variant, mid-ventral surface; (f) detail, chorionic cell and reticulum ventral-lateral portion of transition. Scale = 20 μm (a, b, c), = 10 μm (d, e, f).

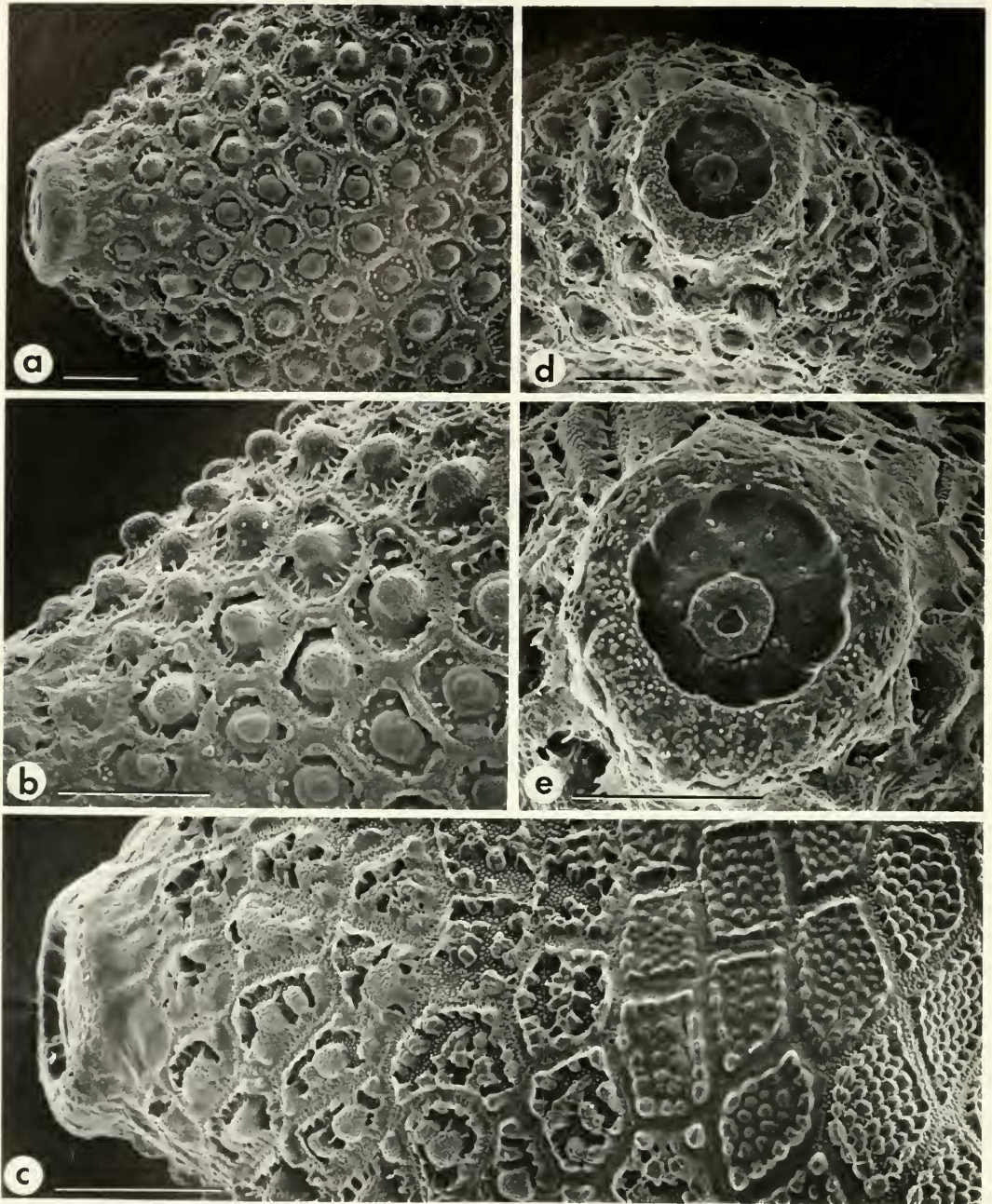


Fig. 11. *Ae. notoscriptus*. (a) Anterior end, ventral surface; (b) anterior end, chorionic cell detail; (c) anterior end, dorsal surface; (d) anterior end and micropylar apparatus; (e) detail, micropylar apparatus. Scale = 20 μ m.

(Table 2), particularly in *Ae. notoscriptus*, where the single large tubercle obviously varied considerably between eggs (Fig. 15). In *Ae. funereus*, large tubercles tended to be

smaller in cells with more than one (Fig. 15), and mean diameters consequently were smaller in eggs (1, 2, 3, Table 2) so structured (Fig. 3).

Numbers of small tubercles per cell differed significantly in both *Ae. notoscriptus* and *Ae. alternans* (Table 2). Only one of the *Ae. notoscriptus* eggs (5) was different from the others, but it had many more small tubercles per cell, as easily distinguishable (Fig. 15). The *Ae. alternans* egg that had most small tubercles (egg 4) was also the one that was the largest of the five (Fig. 15) both in terms of cell length and width (not tabulated). This association might be due to chance, but in all likelihood more small tubercles are present in eggs with cells of larger area. There was considerable variation in the number of small tubercles in this species, as egg 4 did not alone differ significantly from the others (Table 2). In terms of small tubercle size, one egg differed from the remainder in *Ae. funereus* and *Ae. notoscriptus*, while there were no significant differences in *Ae. alternans*.

The relative dimensions of cells, reflected in the length/width ratios, remained fairly consistent within species, with only one egg significantly different from the remainder in *Ae. funereus* and *Ae. notoscriptus*, and none different in *Ae. alternans*. The larger ratio of egg 5 in *Ae. notoscriptus* in fact barely achieved significance from the other four but egg 2 in *Ae. funereus* was considerably longer in relation to width (Table 2). This may have been an unusually long egg, as it was our impression while making the measurements that the cells of long eggs tend to be proportionately longer in the anterior/posterior axis.

DISCUSSION

The description we present here for *Ae. funereus* is apparently the first complete account of the egg of any species in the subgenus *Verrallina*. Matsuo et al. (1974) briefly described the egg of *Ae. (Ver.) butleri* Theobald (including two electron micrographs), but showed only a low power view of approximately the posterior half of the egg and detail of a single chorionic cell on the ventral (upper) surface. No descriptions

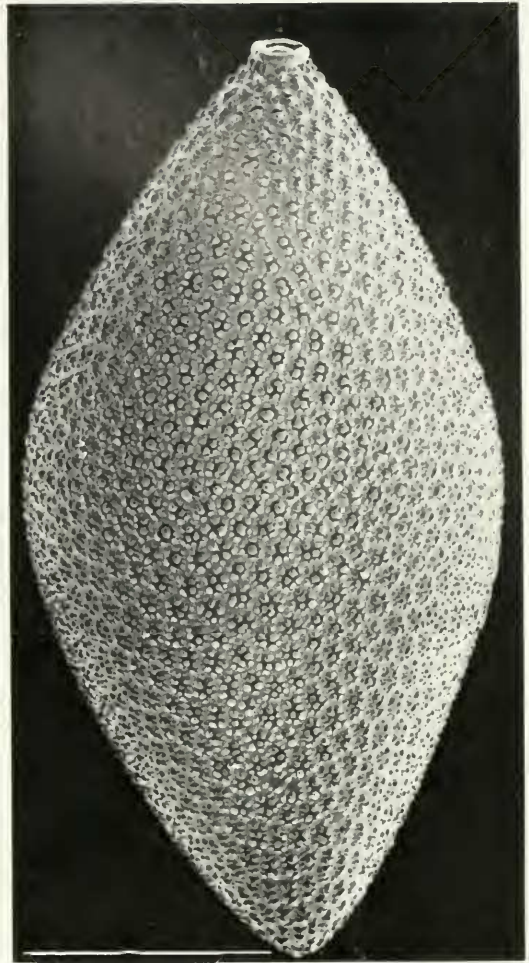
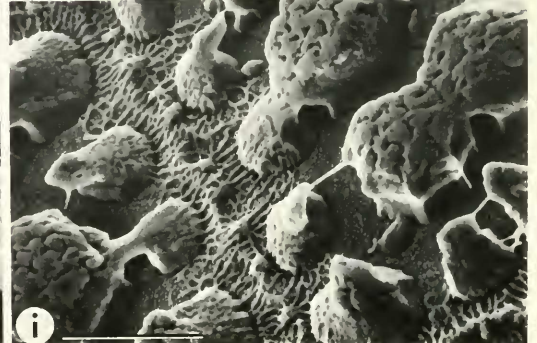
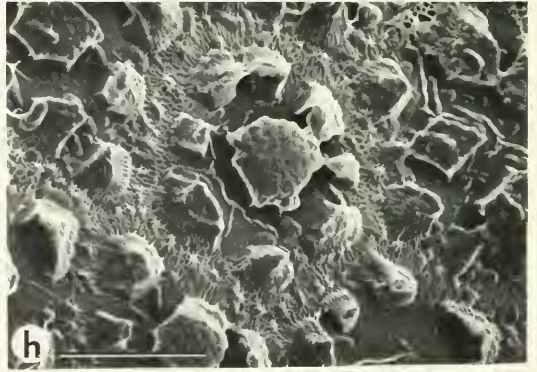
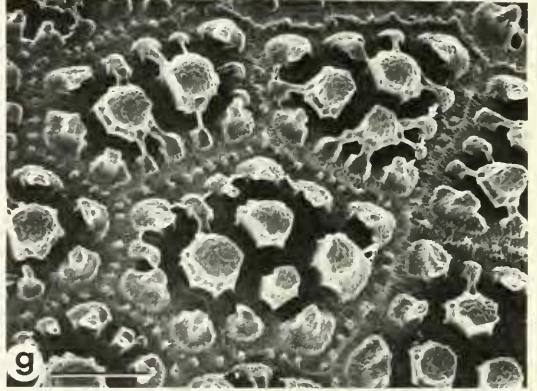
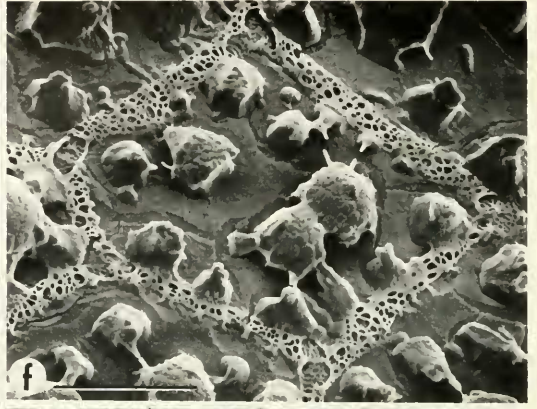
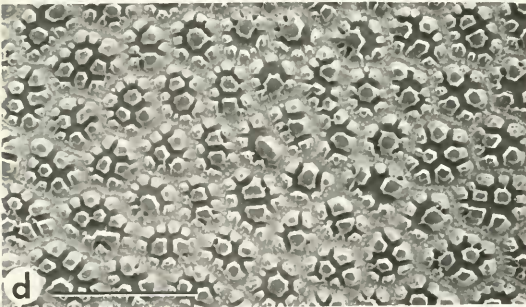
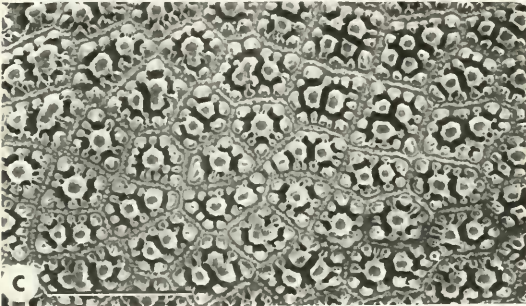
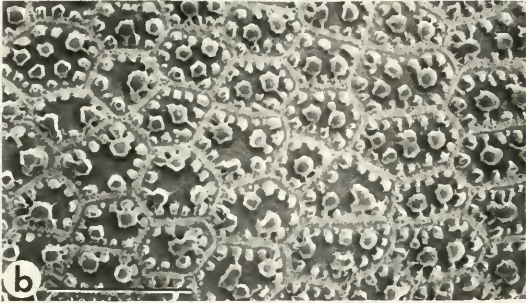
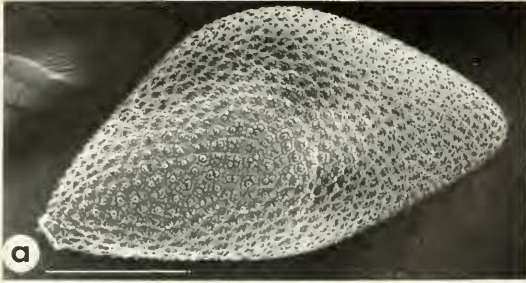


Fig. 12. *Ae. alternans*. Entire egg, ventral (upper) view, anterior end at top. Scale = 200 μm .

or illustrations were given of the anterior end and micropylar apparatus, details of the posterior end, chorionic structure in the ventral-dorsal transition, or dorsal surface. They gave a mean length and width of 667 μm and 172 μm , indicating that this egg is shorter and relatively wider (L/W ratio 3.88) than the egg of *Ae. funereus* (ratio 4.50), which is conspicuously elongated. Both the description and illustration (Matsuo et al. 1974) show that the detailed structure of the outer chorionic cells and tubercles are different in the two species. Large tubercles appear to be more numerous in *Ae. butleri*



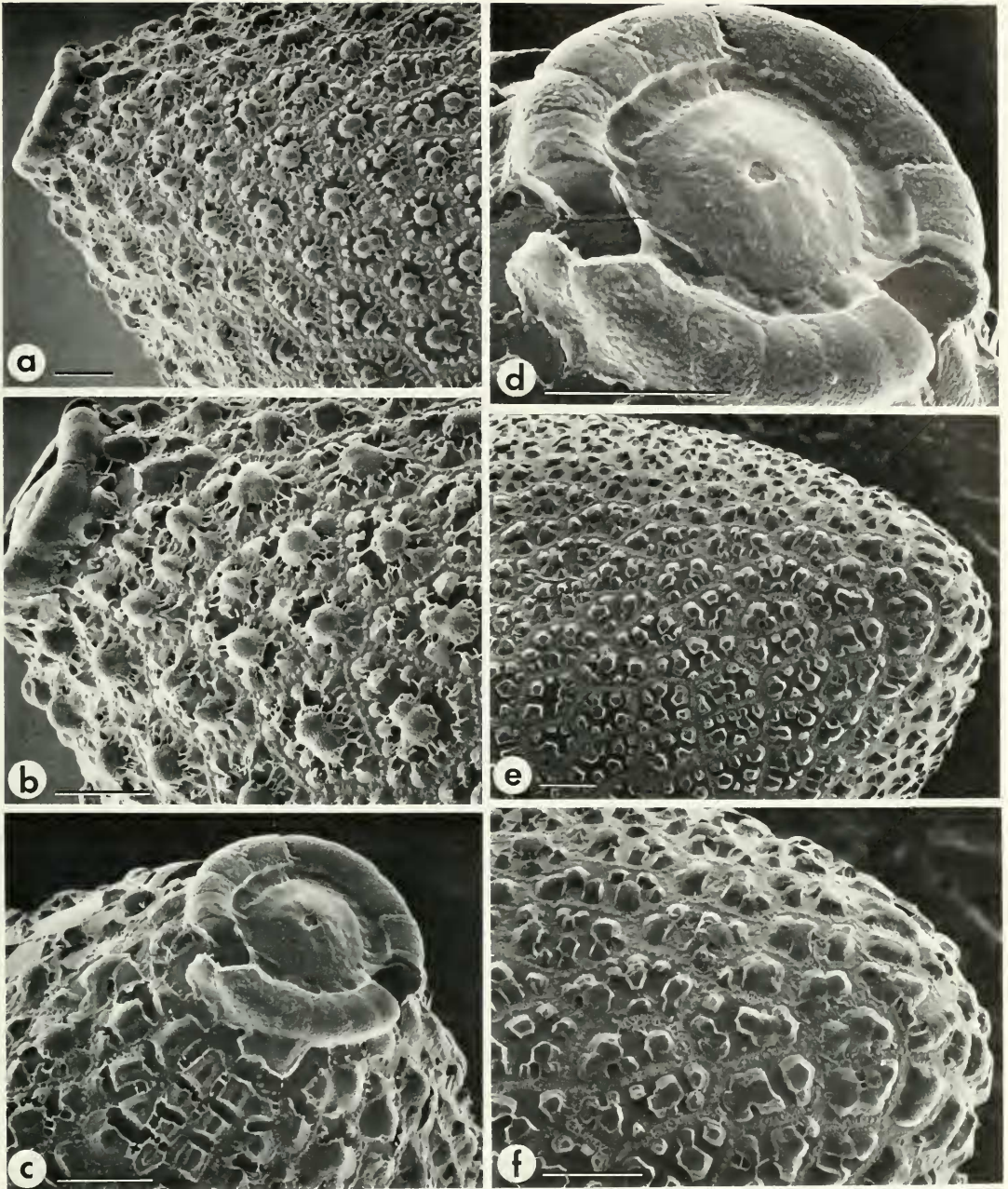
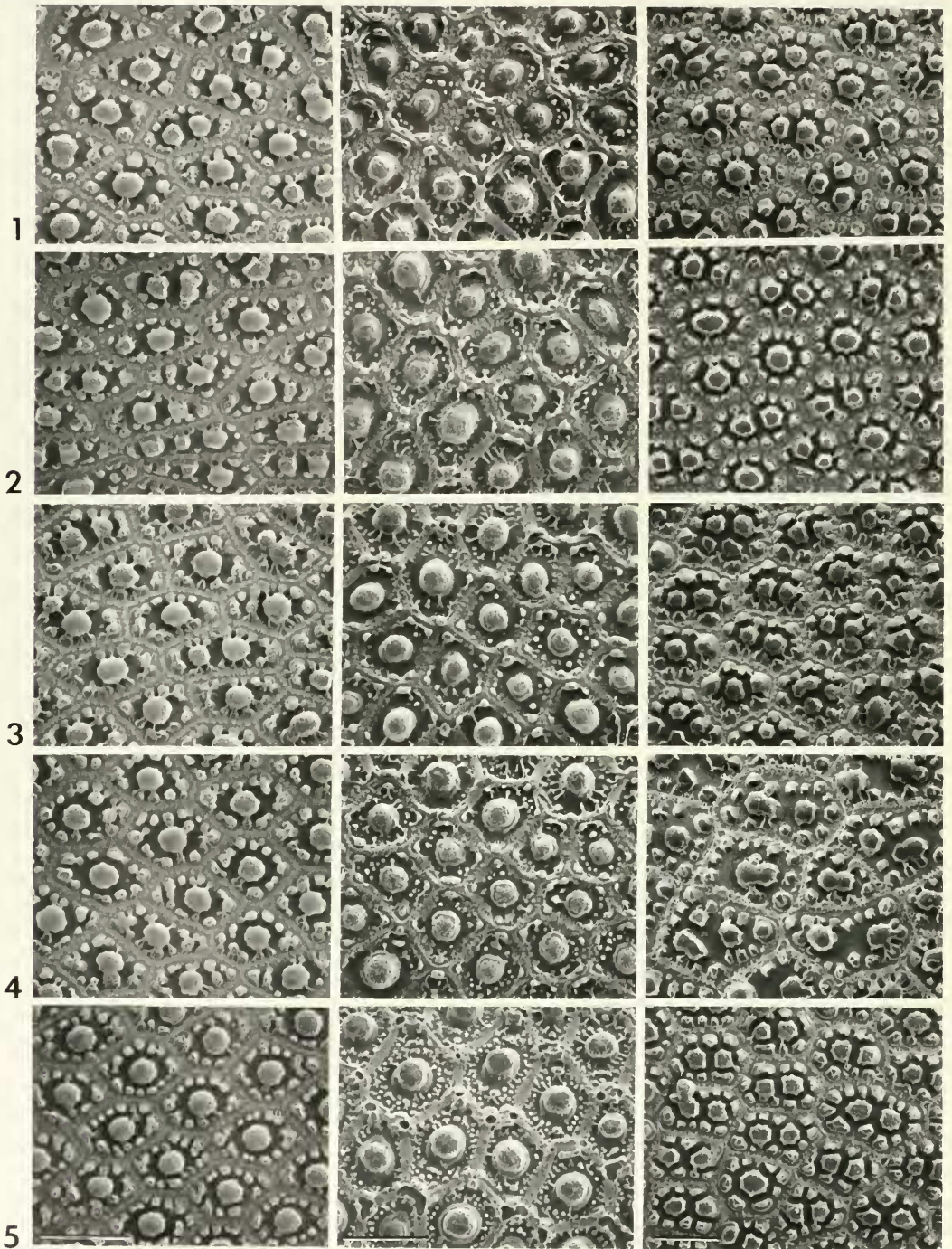


Fig. 14. *Ae. alternans*. (a) Anterior end, lateral surface; (b) anterior end, outer chorionic cell detail; (c) anterior end and micropylar apparatus; (d) detail, micropylar apparatus; (e) posterior end, lateral surface; (f) posterior end, outer chorionic cell detail. Scale = 20 μm .

←
 Fig. 13. *Ae. alternans*. (a) Whole egg, lateral view, anterior end at left; (b) outer chorionic cells, ventral surface, middle of egg; (c) outer chorionic cells, lateral surface; (d) outer chorionic cells, dorsal surface; (e) detail, variant of outer chorionic reticulum; (f) detail, chorionic cell on ventral surface; (g) detail, chorionic cell on lateral surface; (h) detail, chorionic cell on dorsal surface; (i) detail, variant of outer chorionic reticulum and detail of large and small tubercles, ventral surface. Scale = 200 μm (a), = 50 μm (b, c, d), = 10 μm (f, g, h), = 5 μm (e, i).

Egg



Ae. funereus

Ae. notoscriptus

Ae. alternans

and probably smaller in relation to small tubercles, which are less confined to the periphery of the cell field than in *Ae. funereus*.

In previously published descriptions of *Aedes* eggs there has been an almost uniform tendency, for those species that attach their eggs to a substrate, to illustrate only the upper (ventral) surface and ignore the lateral and particularly the dorsal (glued) surfaces. The complex egg of *Ae. notoscriptus* well illustrates how important information can be lost by incomplete examination. In this case the structure of the dorsal (lower) surface is of especial interest. Previous studies of eggs of species in subgenus *Finlaya* have been made with the electron microscope (Matsuo et al. 1972, Moriya et al. 1973), but a recent study of *Ae. togoi* (J. R. Linley and K. L. Chan, personal observations) is the only one in which the dorsal surface was examined. After an abrupt transition from lateral surface structure, the dorsal surface proved to be made up of cells in which many small tubercles had apparently become elongated into adherent filaments extending into adjacent cells and covering the entire dorsal surface. This structure, moreover, is not peculiar to *Ae. togoi*, but is probably common, in various stages of elaboration, within the subgenus *Finlaya*. We have recently examined (unpublished) two other species in this subgenus, *Ae. rubrithorax* (Macquart) and *Ae. alboannulatus* (Macquart). The dorsal surface filaments in these are even more extremely developed, forming dense mats over the lower surface of the egg.

The structure in *Ae. notoscriptus* is interesting in this context because it may represent an early stage in the elaboration of filaments. Filaments as such are absent, but the large tubercles of the ventral surface are replaced by smaller ones and, interspersed

with these and covering the reticulum, many even smaller tubercles that by outgrowth could immediately form a hair-like mat. Linley and Chadee (in press) have pointed out that in *Haemagogus equinus* Theobald and *Hg. janthinomys* Dyar, where highly developed filaments also occur, their presence may enhance anchorage of the egg by effectively increasing the surface area to which cement can adhere at oviposition. Like the two *Haemagogus* species, *Ae. notoscriptus* breeds primarily in small container habitats, both natural and man-made (Lee et al. 1982), where firm adhesion would protect the eggs from removal by predators or the flushing action of heavy rain.

In contrast to the eggs of *Ae. funereus* and *Ae. notoscriptus*, the more or less uniform surface of the egg of *Ae. alternans* indicates that it is probably not affixed with glue to the oviposition surface. Eggs may be laid singly on water (Colledge 1904) or, according to observations by E. N. Marks (see Lee et al. 1984), singly on mud at the edges of drying pools. The pronounced bi-conical shape, with strongly arched ventral surface, conforms to other species in the subgenus (Mattingly 1970), and the structure and arrangement of tubercles in the chorionic cells also appears generally similar. It is impossible, however, to compare the level of detail in electron micrographs with small line drawing (Mattingly 1970), or with Pillai's (1962) illustrations taken from impressions on celloidin.

ACKNOWLEDGMENTS

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Fig. 15. *Ae. funereus*, *Ae. notoscriptus*, *Ae. alternans*. Areas of the outer chorion, ventral surface, middle of egg, for each of 5 individual eggs (numbered on left) of each species. Scale = 20 μ m.

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